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DAILY ENERGY EXPENDITURE OF MALE AND FEMALE MARSH HARRIER NESTLINGS

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ABSTRACT.—We used the doubly labeled water (DLW) method to measure daily energy expenditure (DEE) in eight brother-sister pairs of free-living Marsh Harrier (*Circus aeruginosus*) nestlings. We calculated metabolizable energy intake (ME) from DEE and body-mass change. In each pair, males had lower body mass, DEE, and ME than their female siblings. On average, male body mass was 20%, DEE 19%, and ME 20% lower than that of female siblings. Thus, energy turnover was proportional to body mass. Because the average sex ratio at fledging in Marsh Harriers is 55% male, and the energy requirement of sons is 45% of the son-daughter pair, this sex ratio matches exactly that predicted by Fisher's theory (1930). A literature review revealed that DEE (kJ/day) measured by DLW when nestlings were approximately 95% of asymptotic or fledging mass scaled as $4.58 M^{0.76}$ (where M = body mass in g) in 11 species of altricial nestlings, including the Marsh Harrier. Received 14 November 1996, accepted 3 December 1997.

FISHER'S (1930) THEORY of equal allocation predicts offspring sex ratios at the end of parental care based on the cost of producing a son versus a daughter. This theory, however, does not identify the proximate mechanism that causes the predicted ratios. Apart from recent work on the Seychelles Warbler (*Acrocephalus sechellensis*; Komdeur et al. 1997), there is little evidence that birds can control the sex of their offspring at conception. A possible mechanism for altering the primary sex ratio is differential mortality of the sexes. In species in which males and females grow toward different body masses, energy requirements are expected to be higher for the heavier sex (Richner 1991). If parental investment is equal per unit of energy required, then the larger sex will be more costly to produce. Sex-specific energy requirements may well be instrumental in changing sex ratios at conception by selecting against the more costly sex when food conditions during the period in which parental care is provided are suboptimal.

In several laboratory studies of sexually size-dimorphic altricial species, the sex with the higher adult body mass had the highest energy requirement (Fiala and Congdon 1983, Teather 1987, Frumkin 1988, Anderson et al. 1993, Ben-

nett et al. 1995; but see Collopy 1986). In contrast, field energy requirements of sexually size-dimorphic altricial species are not well established. A field study of Eurasian Sparrowhawk (*Accipiter nisus*) nestlings suggests that the larger sex does not necessarily consume more food (Newton 1978; but see Frumkin 1988). Although the methods used have been criticized (Anderson et al. 1993, Weathers 1996), it is theoretically possible that the smaller sex needs more energy for processes other than growth, such as competition for food, thermoregulation, digestive efficiency, or rate of maturation (Richter 1983, Newgrain et al. 1993). On the other hand, in a study of free-living Rooks (*Corvus frugilegus*), parents invested about 10% more in males (15% heavier) than in females (Slagsvold et al. 1986).

The Marsh Harrier (*Circus aeruginosus*) is a diurnal bird of prey with pronounced reversed sexual size dimorphism (males 540 g, females 737 g; Glutz von Blotzheim et al. 1971). Based on visual observations (i.e. indirect), food intake of free-living male and female Marsh Harrier nestlings during the entire nestling period was equal (Witkowski 1989). In contrast, food intake of hand-reared nestlings determined by weighing over the entire nestling period was higher for females (K. Krijgsveld unpubl. data). Therefore, it is important to establish field energy requirements of nestlings more directly.

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Such information could further contribute to the understanding of the male bias (55%) in fledgling sex ratio in this species (Zijlstra et al. 1992).

In this study, we assessed daily energy expenditure (DEE) of Marsh Harrier nestlings in natural nests where both sexes were present. DEE was estimated using the doubly labeled water (DLW) method (Lifson and McClintock 1966). From these measurements we further estimated metabolizable energy intake (ME) in order to assess the difference in costs between raising males versus females. The results were compared with a study in our laboratory in which Marsh Harrier nestlings were hand-raised under laboratory conditions (K. Krijgsveld unpubl. data).

STUDY AREA AND METHODS

This study was conducted in the Lauwersmeer area of The Netherlands (52°20' N, 6°16' E; Altenburg et al. 1982) from 1990 to 1994. Nests were located throughout the breeding season (mainly during incubation) by observing adult males carrying prey items to the nest. Nests were visited once every three days. Chicks were individually marked at hatching. Body mass was measured using 50-g (± 0.25 g) and 1,000-g (± 1 g) spring balances. Age was known exactly (rounded to one day) or was estimated by a previously established relationship between age and wing chord (Zijlstra et al. 1992). Sex was determined by measuring toe-pad length when individuals were at least 20 days old (Zijlstra et al. 1992). Logistic growth curves were fitted by least-squares regression (SPSS/PC+) using the model:

$$M = A / [1 + e^{-k(\text{Age} - b)}], \quad (1)$$

where M is body mass (g), A is asymptotic body mass (g), k is a constant proportional to overall growth rate (Ricklefs 1968), age is expressed in days, and b is the inflection point in days.

Daily energy expenditure was measured in 1993 using DLW (Lifson and McClintock 1966, Nagy 1980). In eight nests in which both sexes were present, we measured DEE of one male and one female simultaneously. This pairwise design minimizes the effect of factors other than sex (e.g. date, time, brood size, environmental conditions, genetic differences) and enhances statistical power. Nestlings that were obviously in poor condition (i.e. fault bars in feathers, extremely low body mass) were excluded, and none of the broods had a polygynous father provisioning more than one brood. Because Marsh Harriers hatch asynchronously, two successive nestlings within the hatching sequence were selected, both as close as possible to 23 days age. This age was chosen

because on day 23 sex can be determined, recapture is possible, and laboratory energy requirements reach their maximum (K. Krijgsveld unpubl. data). Furthermore, by this age growth rate has decreased, and errors in measuring CO_2 production due to the incorporation of isotopes in newly synthesized tissues should be small (Klaassen et al. 1989, Haggerty et al. 1991, Gabrielsen et al. 1992, Midwood et al. 1993).

Nestlings were injected intraperitoneally with DLW; males received 0.85 mL, females received 1.0 mL. The isotope ratio was 11.7889 gram H_2^{18}O (90.79 AP), 5.7562 gram $^2\text{H}_2\text{O}$ (99.9 AP). An initial blood sample was taken from the vena ulnaris after an equilibration time of 90 min, during which the birds stayed on the nest. A final blood sample was taken approximately 48 h later (range 47.2 to 48.7 h). Four background samples were taken from nonexperimental birds to measure the natural abundance of ^2H and ^{18}O . Blood samples were immediately stored in capillary tubes (250 μL) and flame-sealed. The samples were analyzed by mass spectrometry at the Biomedical Division of the Centre for Isotope Research of the University of Groningen. DEE was calculated (Lifson and McClintock 1966, Nagy 1980) using a factor of 27.5 $\text{kJ L}^{-1} \text{CO}_2$ to convert carbon dioxide production to energy (Gessaman and Nagy 1988).

Metabolizable energy intake was calculated using the following model (Ricklefs 1974):

$$\text{ME} = \text{DEE} + [\Delta M E_d], \quad (2)$$

where ΔM is growth in g day^{-1} and E_d is the energy density of fresh tissue, assumed to be 7 kJ g^{-1} (Ricklefs 1974, Wijnandts 1984, Klaassen 1992, Weathers 1996). Statistical calculations were performed using Statistix 3.1. All within-pair comparisons were tested using two-sided Wilcoxon signed-rank tests.

RESULTS

Body mass and growth.—Body mass of male and female nestlings did not differ before 15 days of age (Fig. 1). From day 15 onward, female nestlings were consistently and significantly heavier than males. Logistic growth curves of males had a significantly earlier inflection point and lower asymptotic body mass than those of females, but the growth constants were not statistically different (Table 1).

Within pairs treated with DLW, male and female nestlings did not differ significantly in either age, number in hatching sequence, or growth rate (Table 2). Every female was heavier than its male sibling. DLW-treated individuals had a slightly (3.5%) but not significantly higher body mass than expected from the logistic growth curve (Wilcoxon signed-rank test, $Z =$

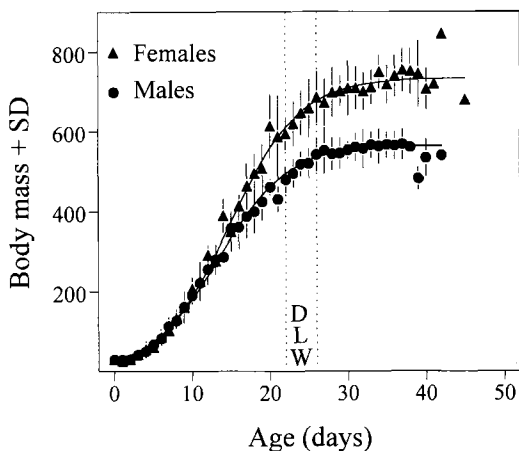


FIG. 1. Growth of free-living Marsh Harrier nestlings. Data points are $\bar{x} \pm 1$ SD of 200 males and 190 females from 130 nests. Lines represent the fitted logistic growth curves. Dotted lines indicate the interval during which DEE was measured. Only data from nestlings that lived until the oldest nestling in the brood was ≥ 35 days are included.

1.69, $P > 0.1$). Body mass of the DLW-treated individuals also was not significantly different from individuals of the same age hand-raised in laboratory conditions ($Z = 1.01$, $P > 0.1$).

Daily energy expenditure.—Within pairs, female nestlings had a higher DEE than male siblings (Fig. 2). Mass-specific DEE did not differ within pairs (males: $1.08 \pm \text{SD of } 0.20 \text{ kJ g}^{-1} \text{ day}^{-1}$; females: $1.07 \pm 0.13 \text{ kJ g}^{-1} \text{ day}^{-1}$). In the pooled values for males and females, DEE (kJ day^{-1}) increased virtually proportionally with body mass (range 455 to 718 g):

$$\text{DEE} = 1.13 M^{0.99} \quad (3)$$

($r^2 = 0.45$, $df = 15$, $P < 0.01$; $s_{yx} = 0.07$, $s_a = 0.82$, $s_b = 0.30$, 95% CI of mass exponent = 0.63).

Metabolizable energy intake.—Like DEE, ME was significantly higher for female nestlings than their male siblings (Fig. 3), and mass-specific ME was not statistically different between

sexes within pairs (males: $1.23 \pm 0.37 \text{ kJ g}^{-1} \text{ day}^{-1}$; females: $1.24 \pm 0.19 \text{ kJ g}^{-1} \text{ day}^{-1}$). For males and females pooled, ME (kJ day^{-1}) scaled with body mass as:

$$\text{ME} = 0.28 M^{1.23} \quad (4)$$

($r^2 = 0.33$, $df = 15$, $P < 0.01$). In a laboratory study, Karen Krijgsveld (unpubl. data) found that males and females ingested on average 954 and 1,148 kJ day^{-1} of food, respectively, at 22 to 26 days of age. She further found an assimilation coefficient of 0.71 (no difference between the sexes), so that ME could be estimated at 677 kJ day^{-1} for males and 815 kJ day^{-1} for females. On average, our estimates of field ME were only 3.2% lower in males and 0.7% higher in females than the laboratory measurements.

DISCUSSION

Marsh Harrier nestlings showed a growth pattern characteristic of birds of prey, with a clear distinction in asymptotic body mass between the sexes and a peak in body mass shortly before fledging (Collopy 1986, Dijkstra et al. 1990, Schaadt and Bird 1993, Negro et al. 1994). In sexually size-dimorphic birds, the smaller sex grows at a relatively faster rate and matures at a higher rate (i.e. point of inflection earlier) than the larger sex, which grows at a higher absolute rate (Teather and Weatherhead 1994). In Marsh Harriers, asymptotic body mass was significantly different between males and females, and absolute growth rate over the entire nestling period averaged 20 g day^{-1} for males and 25 g day^{-1} for females. Furthermore, males reached the point of inflection at an earlier age than females (Table 1). The growth constant was not statistically distinguishable between the sexes, as in the Osprey (*Pandion haliaetus*; Schaadt and Bird 1993). Males matured faster than females, resulting in the capability to fledge at an earlier age (Witkowski 1989, B. Riedstra pers. obs.).

TABLE 1. Parameter estimates ($\pm \text{SE}$) of the logistic growth curve for body mass in Marsh Harrier nestlings. A is asymptotic body mass, k is the growth constant, and b is the inflection point.

	A (g)	k	b (days)	r^2	n^a
Males	546.1 ± 3.25	0.226 ± 0.061	13.4 ± 0.15	0.98	450
Females	734.2 ± 5.04	0.222 ± 0.061	14.8 ± 0.17	0.94	439
Z	31.37	0.05	6.12		
P	<0.001	>0.01	<0.001		

^a Based on 200 males and 190 females from 130 different nests.

TABLE 2. Sex-specific characteristics of DLW-treated nestlings. Data are presented as group means \pm SD. Body mass and age are the mean values between day of injection and day of taking final blood sample. ME is the metabolizable energy intake calculated as the sum of DEE and retained energy (growth), and ME_{D20} is metabolizable energy intake calculated via water dilution rates (see Discussion).

	Males	Females	Z	P
Hatching order	2.0 \pm 0.8	2.3 \pm 1.0	0.56	>0.5
Age (days)	24.5 \pm 0.5	23.9 \pm 0.8	1.47	>0.1
Body mass (g)	529.2 \pm 36.2	661.5 \pm 47.1	2.45	<0.02
Growth rate (g/day)	11.7 \pm 19.4	16.0 \pm 18.9	0.98	>0.3
DEE (kJ/day)	573.3 \pm 117.3	708.7 \pm 106.9	2.45	<0.02
ME (kJ/day)	655.3 \pm 213.0	820.7 \pm 158.1	2.31	<0.03
H ₂ O influx (mL/day)	144.0 \pm 19.4	172.7 \pm 26.7	2.17	<0.03
H ₂ O efflux (mL/day)	135.0 \pm 18.7	159.9 \pm 20.5	2.31	<0.03
ME _{D20} (kJ/day)	833.9 \pm 112.2	997.4 \pm 154.6	2.17	<0.03

The doubly labeled water method has been used to measure field metabolic rate of growing altricial nestlings in only 10 studies in which: (1) measurements were performed in the nestlings' natural physical and social environment, and (2) DEE was analyzed on a mass-specific basis. For interspecific comparison, we calculated DEE of these species at approximately 95% of asymptotic or fledging body mass, and transformed CO₂ production to kJ day⁻¹ using an energy equivalent of 27.5 kJ L⁻¹ CO₂ (Gesaman and Nagy 1988). If DEE was analyzed separately for the sexes, we used mean values pooled for the sexes in the allometric analysis. Only 3 of the 10 studies reported sex-specific metabolic rates (i.e. Fiala and Congdon 1983, Droge et al. 1991, Anderson et al. 1993). As in these three studies, Marsh Harrier nestlings of

the heavier sex had a higher DEE, but mass-specific daily energy expenditure did not differ between the sexes. Mass-specific DEE of Marsh Harrier nestlings (1.08 kJ g⁻¹ day⁻¹), the largest species, was well within the range of values for the other species (from 0.95 kJ g⁻¹ day⁻¹ in Blue-throated Bee-eater [*Merops viridis*], Bryant and Tatner [1990] to 3.18 kJ g⁻¹ day⁻¹ in Red-winged Blackbird [*Agelaius phoeniceus*], Fiala and Congdon [1983]). DEE increased almost proportionally with body mass in Marsh Harriers. Among species (Marsh Harrier included), DEE increased with body mass as 4.58 M^{0.76} (Fig. 4; $r^2 = 0.86$, $n = 11$, $P < 0.001$; $s_{yx} = 0.15$, $s_a = 0.17$, $s_b = 0.10$, 95% CI of mass exponent = 0.23). Estimates of the intercepts and slopes when log (body mass) was regressed against

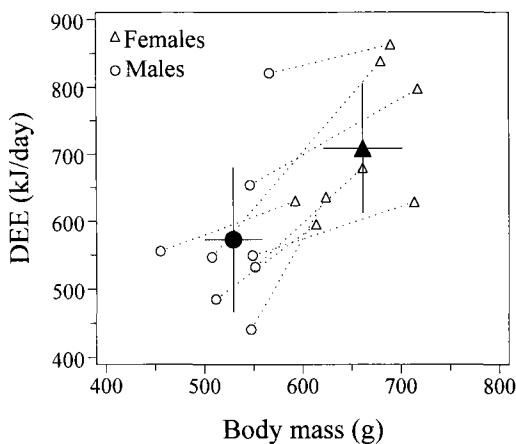


FIG. 2. Daily energy expenditure of free-living Marsh Harrier nestlings. DEE of each male is connected to its sister by a dotted line. Closed symbols represent group means \pm 1 SD.

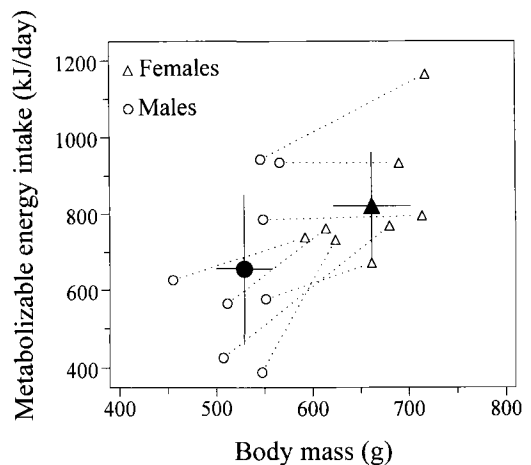


FIG. 3. Metabolizable energy intake of free-living Marsh Harrier nestlings. ME of each male is connected to its sister by a dotted line. Closed symbols represent group means \pm 1 SD.

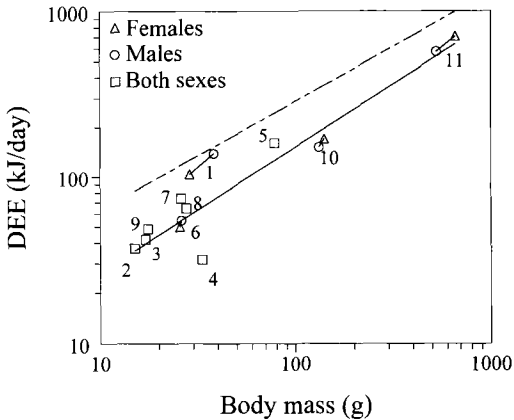


FIG. 4. Scaling of DEE by free-living altricial nestlings measured by DLW as a function of body mass (solid line indicates fitted regression: $DEE = 4.58 M^{0.76}$). The dashed line indicates the DEE of avian parents ($DEE = 13.79 M^{0.66}$; Daan et al. 1990). Open squares represent studies in which DEE was not discriminated between the sexes. In studies discriminating between the sexes, males (open circles) are connected to females (open triangles) by a solid line. (1) Red-winged Blackbird (Fiala and Congdon 1983); (2) House Finch (*Carpodacus mexicanus*; Gettinger et al. 1985); (3) Savannah Sparrow (*Passerculus sandwichensis*; Williams and Nagy 1985, Williams and Prints 1986); (4) Blue-throated Bee-eater (Bryant and Tamer 1990); (5) Acorn Woodpecker (*Melanerpes formicivorus*; Weathers et al. 1990); (6) Eastern Bluebird (*Sialia sialis*; Droge et al. 1991); (7) Ash-throated Flycatcher (*Myiarchus cinerascens*; Mock et al. 1991); (8) Western Bluebird (*Sialia mexicana*; Mock et al. 1991); (9) Yellow-eyed Junco (*Junco phaeonotus*; Weathers and Sullivan 1991); (10) American Kestrel (*Falco sparverius*; Anderson et al. 1993), and (11) Marsh Harrier (this study).

log (DEE) overlapped in comparisons among species and within Marsh Harriers. Therefore, the data are consistent with the idea that DEE varies proportionally with body mass in Marsh Harriers.

If all water ingested by a nestling originates exclusively from food items, then one can estimate ME from deuterium turnover rates, given the water and energy content of the prey (Fiala and Congdon 1983, Williams and Nagy 1985). Assuming 72.8% water content, 5.94 kJ g^{-1} fresh mass of prey (Masman 1986), and an assimilation quotient of 0.71 (K. Krijgsveld unpubl. data), mean ME of all Marsh Harrier nestlings (males and females pooled) is estimated as 916 kJ day^{-1} , which is 177.4 kJ day^{-1} higher

than the average ME derived from DEE and body-mass changes (Table 2). Every mL of water obtained by other means (i.e. by drinking) is wrongly counted as 8.2 kJ (energy content/water content). The difference between the two estimates suggests that Marsh Harrier nestlings drank at least 21.5 mL of water. It is likely that Marsh Harrier nestlings ingested free water via rain, because every measured pair experienced at least one rain shower during the measuring period. Thus, in accordance with Fiala and Congdon (1983), we believe that estimating ME via deuterium turnover rates is unrealistic in our case.

Mean metabolizable energy intake in the field derived from DEE and body-mass changes is similar to ME measured in the laboratory (K. Krijgsveld unpubl. data). This does not mean that conditions (e.g. weather, prey availability, etc.) in the field were optimal for growth. For example, two males and two females treated with DLW decreased in body mass during the measurement period. Moreover, about 30% of all hatchlings in our study area died before fledging due to starvation (Zijlstra et al. 1992), suggesting that food was scarce.

Clearly, we cannot derive estimates of total energy requirements over the entire period from hatching to fledging from measurements of DEE and ME taken during a small part (age 22 to 26 days) of the nestling period. Our data suggest, however, that energy expenditure is directly proportional to body mass. If this proportionality holds for all ages, then the integrated body mass over the whole nestling period of males and females would yield a coarse estimate of relative energy requirements for the two sexes. Assuming a nestling period of 40 days (Witkowski 1989), we calculated the integrated mass of males to be 14,419 g-days and that of females to be 18,393 g-days. The ratio of integrated mass (male/female) is 0.784. Thus, we estimate the ratio of energy requirements of sons versus daughters to be 0.784.

Fisher's (1930) theory predicts that for populations, the total investment in all sons should equal the investment in all daughters. Neglecting the period of postfledging care, the population sex ratio of Marsh Harriers at fledging can thus be predicted as 1 divided by 0.784, or 1.226 males per female. This prediction closely matches the observed overall sex ratio of fledg-

lings in our study area, which is 1.222 males per female (Zijlstra et al. 1992).

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